

RESEARCH ARTICLE

Effects of different amounts of micro-sprinkler irrigation on the yield and quality of *Morchella* in Linxia Hui Autonomous Prefecture

Bo Xing^{1,2}, Chunxia Wang³, Jian Zheng^{1,2,*}, Yun Yang³, Xiongfei Hou³

¹College of Energy and Power Engineering, Lanzhou University of Technology, Lanzhou, Gansu, China. ²Key Laboratory of Complementary Energy System of Biomass and Solar Energy, Lanzhou, Gansu, China. ³Water Conservancy Science Research Institute of Linxia Hui Autonomous Prefecture, Linxia, Gansu, China.

Received: December 10, 2024; accepted: April 7, 2025.

Different amounts of micro-sprinkler irrigation have certain impacts not only on the soil habitats of cultivated morel mushrooms, but also on the yield and quality of morel mushrooms. To investigate the yield and quality response patterns of morel mushrooms subjected to different amounts of micro-sprinkler irrigation in Linxia Prefecture and determine optimal irrigation levels for the main morel planting soils in this region, five irrigation treatments were set up as local irrigation amount (CK), 95% of CK (T1), 90% of CK (T2), 85% of CK (T3), and 80% of CK (T4). The impact of different irrigation amounts on the physical and chemical characteristics of soil as well as yield and quality of morel under micro-sprinkler conditions were evaluated. Principal component analysis (PCA) was applied to conduct a comprehensive evaluation on the yield and quality of morel. The results revealed that micro-sprinkler irrigation significantly increased soil moisture in the depth range of 0 - 10 cm, while the influence of various irrigation volumes on soil temperature at a constant depth was found to be negligible. The soil temperature range of 5 – 10°C in the experimental area during winter was found to be more conducive to the later growth of mycelium and formation of fruiting bodies. Organic carbon content presented different trends in different planting soils. In yellow loam soil, organic carbon initially increased and then decreased, while in black soil, there were little variations in organic carbon content. With the increase of the amount of irrigation from micro-sprinkler irrigation, morel mushroom yield was increased. However, the quality indicators declined. Soil organic carbon, available potassium content, soil moisture, and ambient temperature were positively correlated with high morel yields. PCA evaluation results indicated that T2 treatment (90% CK) achieved a balance between the yield and quality of morel mushrooms in both yellow loam and black soil with black soil being more favorable in terms of morel mushroom yield and quality compared to yellow loam soil.

Keywords: *Morchella*; micro-sprinkler irrigation; yield and quality; comprehensive evaluation.

*Corresponding author: Jian Zheng, College of Energy and Power Engineering, Lanzhou University of Technology, Lanzhou 730050, Gansu, China. Email: pojianilb645@163.com.

Introduction

Morel mushrooms taste delicious and contain amino acids, fat, organic acids, minerals, and other nutrients with antioxidant, anti-

inflammatory, and anti-tumor bioactivity [1], which can be employed as both edible mushroom and traditional Chinese medicine [2]. In 2018, Linxia Prefecture, Gansu, China began to introduce and plant this product on large scale.

Morel mushrooms belong to low-temperature saprotrophic mycorrhizal fungi family with more stringent sensitivity to growing temperature, environment humidity, and soil habitat conditions including soil water content, temperature, nutrients, *etc.* [3]. Sichuan and Chongqing regions are the first regions to carry out large-scale cultivation of morel mushrooms, therefore, planting management experience is more mature in these regions. After the introduction of morels into Linxia, water, nutrient, and temperature management in the Sichuan-Chongqing area has been considered as references. However, Linxia locates in Loess Plateau - Qinghai-Tibet Plateau transitional zone with high altitudes above 1,500 m and a cold climate with average annual temperature range of 5.6 - 9.7°C [4]. Hence, greenhouse cultivation is commonly applied for this product [5]. Significant differences are also observed in planting soils. The most common planting soils in the Sichuan-Chongqing area are purple, brown, and yellow soils, which have loose texture and high amounts of organic matter. Linxia Prefecture primarily has black and yellow loam soils, which have high clay contents and are prone to clumping. Consequently, after introducing open-air model of irrigation management from Sichuan-Chongqing regions, there has been an obvious phenomenon of "not accustomed the climate of a place". Unreasonable amounts of irrigation water resulting in the "gambling" attribute of morel production and some production areas have even experienced the reality of 30 - 50% area being out of harvest. Therefore, research on the appropriate levels of irrigation for the main planting soils under morel cultivation conditions in Linxia Prefecture is essential and can provide a foundation for localizing morel cultivation management models in this region.

Environmental temperature, humidity, and soil habitat conditions including soil water content, temperature, nutrients, *etc.* are key factors in improving morel mushroom quality and efficiency [6], which are greatly influenced by the amount and method of irrigation. The morels

actual production in Linxia Hui Prefecture uses traditional ground irrigation, which requires large water volume, has low irrigation uniformity and high requirements for land leveling, the environmental temperature and humidity, and faces difficulties in meeting more stringent requirements in terms of environmental temperature, humidity, and soil habitat conditions necessary for morel growth. Compared with traditional surface irrigation, micro-sprinkler irrigation technology has lower requirements for land flatness and provides higher irrigation uniformity, which can not only replenish soil water and improve soil habitat conditions, but also effectively cool and humidify the soil, regulate the temperature, and wet the environment in greenhouse [7], therefore, is very suitable for the regulation of the growing environments of fungal crops and soil habitat conditions. However, the ambient temperature during morel growing season in Linxia Prefecture is relatively low. Few research works are available on whether micro-sprinkler irrigation technology can meet morel growth and soil environment requirements.

This research investigated the cultivation of morel mushroom in Jishishan County and Linxia County, both located in Linxia Prefecture, Gansu, China. Considering traditional irrigation amount as the control and time as reference, four irrigation amount treatments were set up for the mycelium and seedling stages of morel mushrooms employing micro-sprinkler irrigation technology. The main goal of this research was to examine the impacts of different irrigation volumes on several soil parameters including moisture content, temperature, pH, organic carbon level, total nitrogen content, and available potassium in the primary morel planting soils in Linxia Prefecture under greenhouse conditions. The research also explored the yield and quality response characteristics of morel under different irrigation amounts. In addition, principal component analysis (PCA) was applied to comprehensively evaluate the yield and quality of morel to determine optimal irrigation levels for primary morel planting soils under

micro-sprinkler irrigation. This research would provide a theoretical basis to develop an appropriate irrigation management model for morel cultivation in Linxia Prefecture.

Materials and methods

Study area

This research was conducted from October 2023 to May 2024 at the demonstration base of the edible mushroom industry technology system in Xiaoguan Township, Jishishan Bao'an, Dongxiang, and Salar Autonomous County (also known as Jishishan County), Linxia Hui Autonomous Prefecture, Gansu Province (35°35'N, 102°54'E), and Yinji Town, Linxia County, Linxia Hui Autonomous Prefecture, Gansu Province (35°25'N, 103°02'E). The altitude of the test site varied from 2,200 to 2,500 m. Jishishan County has a typical continental monsoon climate with average annual temperature of 3.68°C, average annual precipitation of 660.2 mm, and average annual evapotranspiration of about 880 mm. Linxia County has a transition zone climate between temperate semi-humid and alpine humid zones with 5.9°C average annual temperature, 630.6 mm average annual precipitation, and 541.9 mm average annual evapotranspiration. Jishishan test area has jute soil and Linxia County test area possesses black clay soil.

Experimental design and process

All experiments were conducted in greenhouses where inoculation with morel mushroom had not been performed. The test site in Xiaoguan Township, Jishishan County (XG) was a cold greenhouse and that in Yinji Town, Linxia County (YJ) was a warm greenhouse. Sheep belly mushroom planting and pest control complied with local planting methods and all test varieties were six sister sheep belly mushrooms. In XG test site, the plot layout and land preparation commenced on October 5, 2023 by drawing the lines to open borders with 120 cm width, 15 cm height, and 30 cm spacing, and sown with morel mushrooms by furrow sowing on October 9,

2023. On November 2, 2023, exogenous nutrient bags were placed in a "zigzag" arrangement with the frequency of 3 to 4 bags per square meter. On November 9, 2023, plastic films were covered, allowing the mycelium to enter hibernation. This site entered the primordium stage on April 29, 2024, while harvesting started on May 23, 2024, and was completed on June 29, 2024. The plot layout and land preparation in YJ test site began on November 16, 2023, and sowing was performed on November 17, 2023. Exogenous nutrient bags were placed on November 25, 2023, with the frequency of 3 to 4 bags per square meter. This site entered primordium stage on March 11, 2024, Harvesting started on April 6, 2024, and was completed on May 17, 2024. Test plots were 2 m long and 1.2 m wide with waterproof plastic films buried around the perimeter at 50 cm depth. After sowing, high amounts of water irrigation were necessary for late morel mushroom production. However, irrigation was not suitable after the formation of the original base. Consequently, in this research, no additional moisture treatment was conducted for irrigation after sowing. Considering the water use period in experimental areas, irrigation times followed local habits. Based on local traditional irrigation amount (CK), four irrigation amount treatments were set as 95% of CK (T1), 90% of CK (T2), 85% of CK (T3), and 80% of CK (T4). Each treatment was replicated three times, and the average values were reported as the outcome.

Measurement of soil indicators

RS-TRREC-N01-1 soil moisture meter (Jianda Renke Electronic Technology Co., Ltd., Jinan, Shandong, China) was employed for the determination of soil water content and temperature at 5 cm depth in surface layer. In addition, a geothermometer (Jixing Instrument Factory, Tianjin, China) was applied to measure temperature at 10 cm depth within the soil at a frequency of every 7 days. Soil water content was evaluated through drying method at each morel mushroom growth stage as well as before and after irrigation events. The XG test site had a cold shed, and the monitoring activities were

Table 1. Soil nutrient content in two experimental areas (mean \pm standard deviation).

Experimental area	Organic carbon (g/kg)	Total nitrogen (g/kg)	Available potassium (mg/g)	pH
XG	4.67 \pm 0.56	6.44 \pm 0.894	158.64 \pm 3.268	8.1 \pm 0.124
YJ	17.972 \pm 1.352	5.38 \pm 0.607	217.57 \pm 2.919	7.76 \pm 0.013

suspended on December 14, 2023, due to soil freezing and resumed on April 3, 2024. A soil auger was used to collect soil samples from 0 - 10 cm depth in each plot. Sampling was performed before sowing, at each morel mushroom growth stage, before and after irrigation treatments, and after harvesting. The samples obtained were air dried followed by crushing and sieving through a 2 mm mesh for subsequent analyses. Total nitrogen content in the soil was measured using Kjeldahl method, and soil organic carbon was measured according to potassium dichromate volumetric method, specifically external heating approach. Soil pH was assessed using a DDSJ-308F detector (Leizhi, Shanghai, China) [8]. Quick-acting potassium (AK) was determined through ammonium acetate leaching and analyzed using FSP6650 flame photometry (Yuefeng, Shanghai, China) [9].

Determination of morel mushroom yield and quality

The number of substrates in each experimental plot was counted. The lengths of dried substrate caps and stems were measured using vernier calipers with 0.02 mm accuracy, and cap circumference was measured using a soft ruler with 1 mm accuracy. Substrate fresh and dry weights were obtained using an electronic balance with 0.01 g sensitivity. For each treatment, moisture content was measured in some randomly selected fresh morel mushroom substrates with good quality [10]. The fruiting bodies to be tested were dried in hot air at 40°C for 1.5 hours followed by 50°C \pm 2°C for 8 hours. After drying, ash contents were determined by high-temperature incineration, while crude fiber contents were measured by sulfuric acid-sodium hydroxide washing and ashing. Crude proteins were obtained according to Kjeldahl method, and crude polysaccharides were determined by

spectrophotometry [11]. Furthermore, the quantitative analysis of free phenols was performed using Folin-Ciocalteu method [12].

Comprehensive evaluation of morel mushrooms

Principal component analysis (PCA) was applied to comprehensively evaluate the yield and quality of morel to determine optimal irrigation levels for primary morel planting soils under micro-sprinkler irrigation.

Statistical analysis

Microsoft Excel 2010 (Microsoft, Redmond, WA, USA) was applied to organize the data. SPSS version 27.0 (IBM, Armonk, NY, USA) was employed for statistical analysis of experimental data. PCA was performed and plots were drawn using GraphPad Prism software (version 10) (<https://www.graphpad.com/>). One-way analysis of variance (ANOVA) and Bonferroni's method were used for ANOVA and multiple comparisons, respectively. Plots were drawn using Origin (version 2024b) (<https://www.originlab.com/>).

Results

The soil properties and the irrigation amount at the test sites

The soil properties of the test areas were summarized in Table 1, while the amount of irrigation at each test site were listed in Table 2.

Soil moisture content

The results demonstrated that, before differential irrigation using micro-sprinkler irrigation, soil water content at 0 – 10 cm in each experimental site plot in XG ranged from 19 - 21%. Following the first differential irrigation, soil water content significantly increased with the largest increases ranging from 16 - 22% above the

Table 2. Irrigation in two experimental areas (irrigation capacity /mm).

Experimental area	Growth stages of morel mushroom		Treatments				
			T1	T2	T3	T4	CK
XG	Post-sowing	2023-10-13	45.34	45.34	45.34	45.34	45.34
	Mycelial stage	2023-11-07	14.22	14.22	14.22	14.22	14.22
		2024-05-17	43.04	40.78	38.51	36.25	45.31
	Substrate stage	2024-06-15	39.48	37.4	35.33	33.25	41.56
YJ	Post-sowing	2023-11-17	11.98	11.98	11.98	11.98	11.98
	Mycelial stage	2024-01-09	7.54	7.54	7.54	7.54	7.54
		2024-02-25	51.34	48.64	45.93	43.23	54.04
	Substrate stage	2024-04-30	50.14	47.5	44.86	42.22	52.78

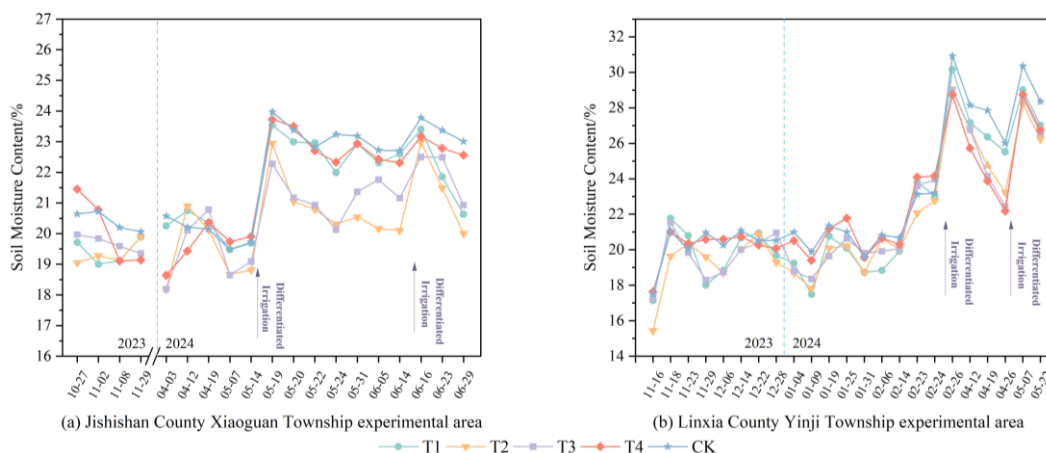


Figure 1. Changes in soil moisture from 0-10 cm.

pre-irrigation levels. After the second differentiated irrigation, soil water content further increased by 3 - 14%. Notably, treatments CK, T1, and T4 had higher soil water contents than treatments T2 and T3. Similar results were obtained at both test sites (Figure 1). Specifically, following the first differentiated irrigation, soil water content in the plots at 0 – 10 cm increased by 19 - 33% and the corresponding values after the second irrigation were 13 - 29%, respectively. After differentiated irrigation, soil moisture content increased with the amount of irrigation, showing a trend of CK > T1 > T2 > T3 > T4 in terms of final soil water content level.

Soil temperature

Soil temperatures measured in the depth of 5 and 10 cm in both experimental sites demonstrated a pattern of initial decline followed by subsequent

increase. Throughout the entire morel mushroom cultivation period, soil temperature curves for depth range of 0 – 10 cm for differentially irrigated treatments almost overlapped (Figure 2). The YJ test site was a warm greenhouse, where soil temperatures at 5 and 10 cm depths ranged from 1 - 19°C. These soil temperatures remained relatively unchanged between 5 - 10°C until January 2024. However, in the XG test site, soil temperature decreased from about 10°C in October 2023 to about 1°C in December 2023, and the soil remained frozen until the end of March 2024. Because of this ground temperature difference, the cumulative temperature required for morel mushroom growth in YJ test area was reached earlier, resulting in an earlier mushroom emergence and longer mushroom emergence period.

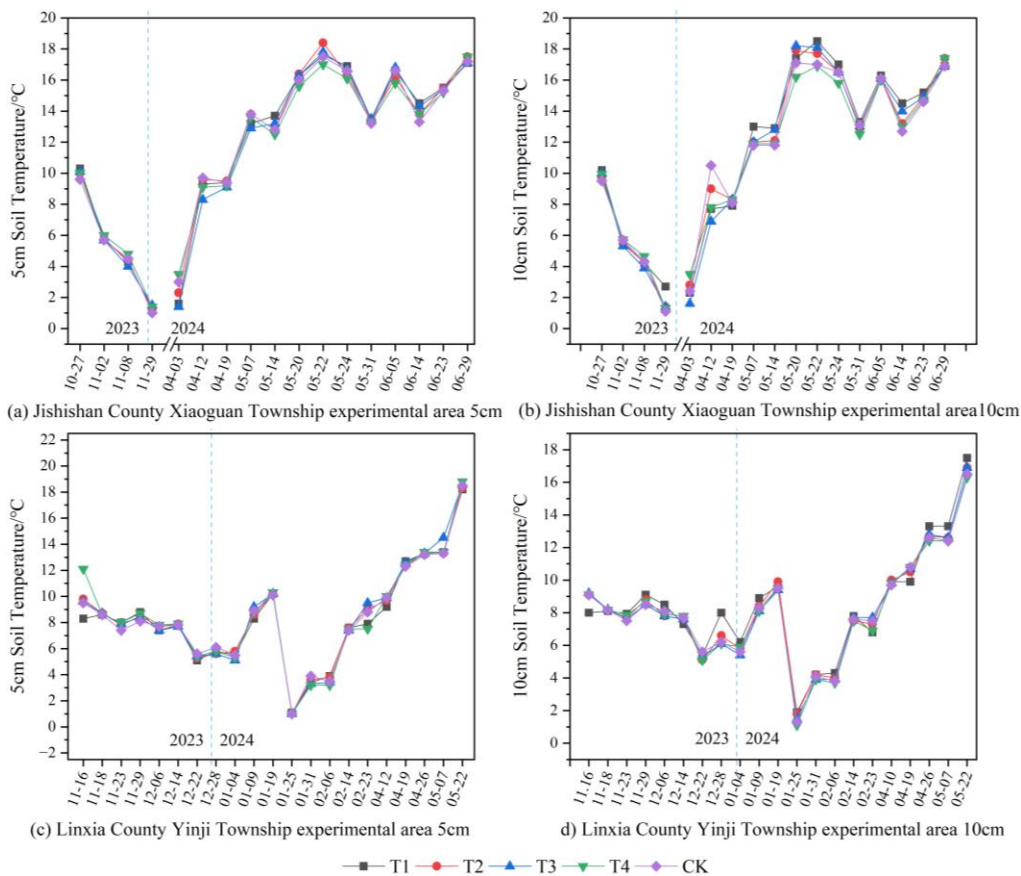


Figure 2. Changes in soil temperatures within the 5 cm and 10 cm soil strata.

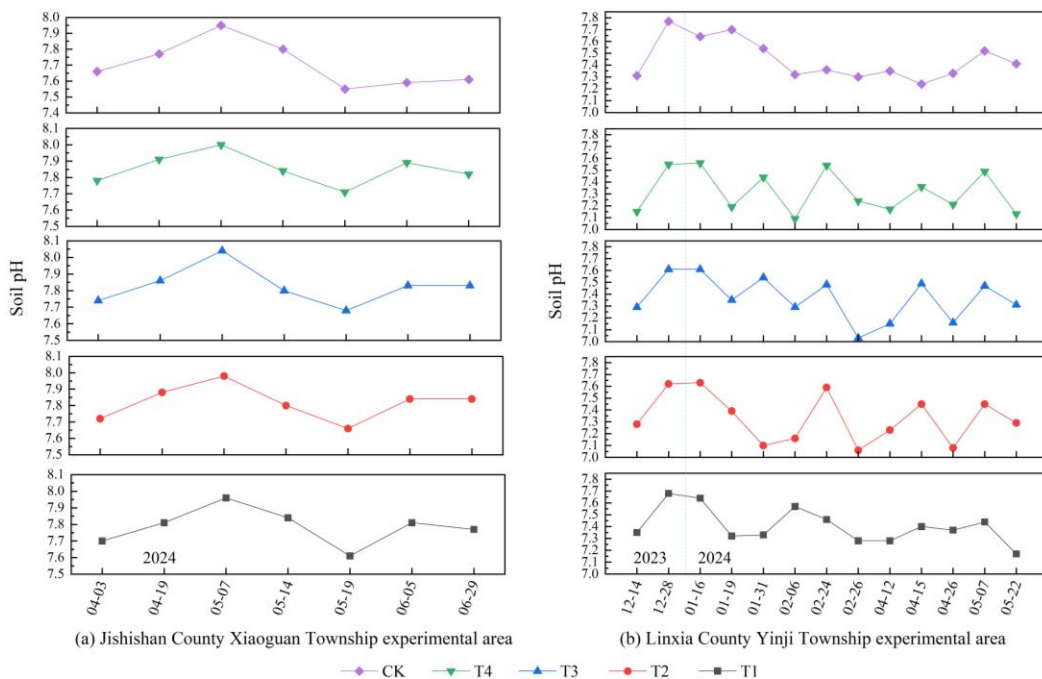


Figure 3. Changes in soil pH values.

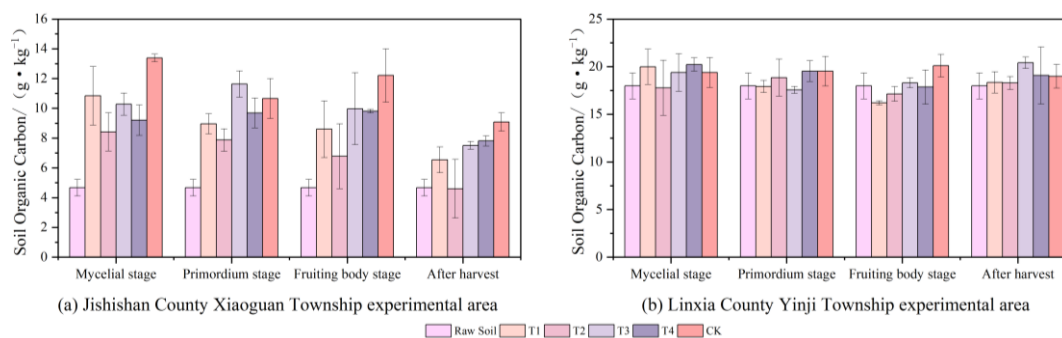


Figure 4. Changes in soil organic carbon content.

Soil pH value

The pH change trends in different treatments on the XG experimental site were consistent. Before irrigation at different amounts, soil pH value in 0 - 10 cm depth ranged from 7.7 to 8.0. After irrigation, soil pH slightly decreased from 1.5 - 3.2%. In treatment CK, soil pH fluctuation range changed from 7.66 - 7.80 before irrigation to 7.55 - 7.61 after irrigation. In YJ experimental site, soil pH value in 0 - 10 cm depth ranged from 7.03 to 7.77 before irrigation. Similarly, after irrigation, soil pH value at the same depth range decreased by 0.8 - 6.9% relative to pre-irrigation pH value. For CK and T1 treatments, soil pH value after irrigation fluctuated within the range of 7.3 - 7.7 before irrigation to 7.3 - 7.5 after irrigation (Figure 3).

Soil organic carbon

The soil in XG test site was jute soil, which had low organic carbon contents. After inoculation with morel mushroom, organic carbon content in 0 - 10 cm soil layer significantly increased from 3.75 to 8.71 g/kg during mycelium stage, while, during morel mushroom reproductive period, soil organic carbon content demonstrated an initially increasing and then decreasing trend. However, at the end of the experiment, soil organic carbon content was still higher than that before inoculation. The cultivated soil in YJ test site was black clay with high content of organic carbon. During morel mushroom fertility period, organic carbon content in 0 - 10 cm soil layer did not change significantly with the range of 16.20 - 20.40 g/kg (Figure 4).

Soil total nitrogen

The comparison of soil total carbon contents before and after inoculation of morel mushrooms showed that there were 6.44 ± 0.894 g/kg in XG test site and 5.38 ± 0.607 g/kg in YJ test site before inoculation, and the total nitrogen contents in 0 - 10 cm soil layers in both sites were decreased after inoculation (Figure 5). The results indicated that the growth and development of morel mushrooms required total nitrogen from soil. Further, the study revealed that morel mushrooms primarily consumed soil total nitrogen during mycelial and primordium stages. Specifically, in XG test site, soil total nitrogen in 0 - 10 cm layer decreased by 2.15 to 3.27 g/kg during mycelial stage and by 0.28 to 1.73 g/kg during primordium stage. In YJ test site, soil total nitrogen decreased by 0.57 to 1.46 g/kg during mycelial stage and by 0.51 to 1.17 g/kg during primordium stage. However, during fruiting body stage, soil total nitrogen content increased slowly. Across all treatments, soil total nitrogen content in 0 - 10 cm layer remained almost unchanged throughout the various growth periods.

Soil available potassium

Soil available potassium content in the 0 - 10 cm layer of XG test site was not changed significantly throughout physiological growth periods with variations range of 125.3 to 194 mg/kg. In all growth periods, soil available potassium contents in treatments T1 and CK were relatively higher than those in other treatments. In YJ test site, soil available potassium content was higher than that

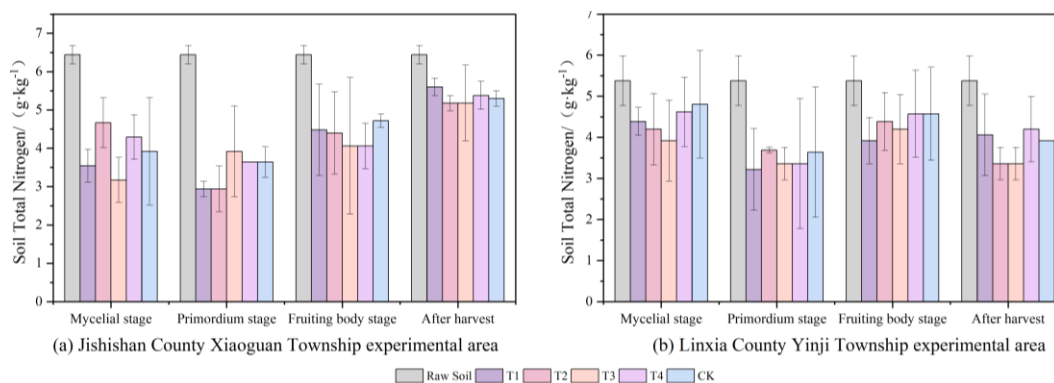


Figure 5. Changes in soil total nitrogen content.

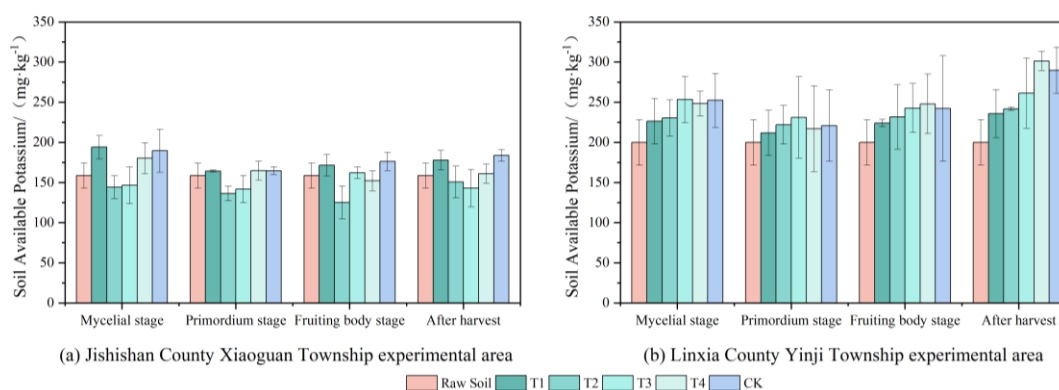


Figure 6. Changes in soil available potassium content.

of the original soil in all growth periods, reaching its highest level in post-harvest period with an increase from 35.79 to 101.4 mg/kg above the original level. Soil available potassium content in treatment T1 was the lowest among all treatments throughout the entire process (Figure 6).

Morel mushroom production

Mushroom density was changed with the trend of CK > T1 > T2 > T4 > T3. Dry and fresh mushroom yields in XG test site and optimal treatment CK were 30.42 mushrooms/m², 43.83 g/m², and 412.3 g/m², respectively. In YJ test site, mushroom density in different treatments was changed as CK > T1 > T4 > T2 > T3 with optimal treatment CK showing the value of 39.58/m². Also, dry mushroom yield in different treatments was changed as T1 > CK > T2 > T3 > T4 with the

optimal treatment T1's value of 84.91 g/m². Fresh mushroom yield in different treatments was as CK > T1 > T2 > T4 > T3 with the optimal treatment CK's value of 824 g/m² (Table 3). The YJ test site was superior to XG test site in terms of mushroom density and dry and fresh mushroom yields, which might relate to the differences in climate, cultivated soil, ambient temperature, and humidity between the two test sites. The differences of mean dry weight of ascospores among different treatments in XG test site were not significant ($P > 0.05$). The observed variation trend was T2 > T3 > T4 > T1 > CK with the maximum value of 1.75 ± 0.65 g. Similarly, differences of substrate length among various treatments were not significant ($P > 0.05$) with the maximum value of 6.28 ± 1.48 cm. For both cap length and cap circumference, the trend was T2 > T3 > T4 > T1 > CK with the maximum

Table 3. Yield of Morel in two experimental areas.

Site	Treatment	Number of healthy substrates (pcs)	Mushroom density (pcs/m ²)	Dried mushroom production (g/m ²)	Fresh mushroom production (g/m ²)
XG	T1	62	25.83	43.72	406.720
	T2	59	24.58	43.14	395.760
	T3	51	22.92	38.57	358.790
	T4	53	24.17	40.73	350.810
	CK	73	30.42	43.83	412.300
YJ	T1	89	37.08	84.91	813.336
	T2	81	33.75	81.85	789.336
	T3	80	33.33	80.18	743.112
	T4	85	35.42	78.23	750.000
	CK	95	39.58	84.38	824.000

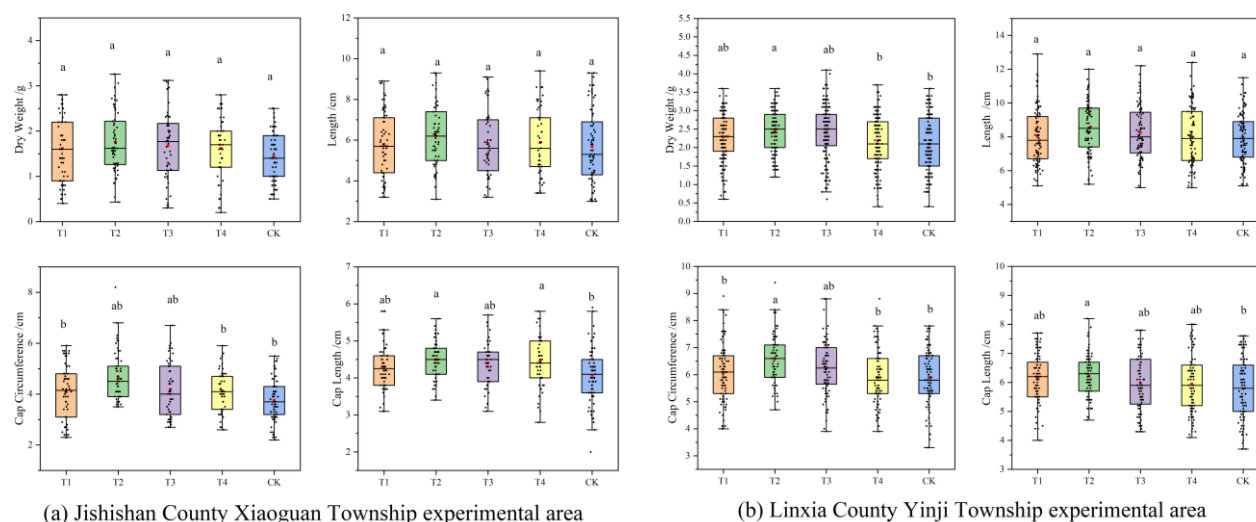


Figure 7. Agronomic traits of morels. The different lowercase letters indicated significant differences among treatments ($P < 0.05$).

values of 4.68 ± 0.95 cm and 4.51 ± 0.48 cm, respectively (Figure 7). In YJ test site, substrate dry weight and cap circumference followed the trend of $T2 > T3 > T1 > T4 > CK$ with the maximum values of 2.43 ± 0.55 g and 6.21 ± 0.74 cm, respectively. Substrate length was similar to that in XG test site, and differences among treatments were not significant ($P > 0.05$) with the maximum value of 8.61 ± 1.54 cm. For cap length, variation trend was $T2 > T3 > T4 > T1 > CK$ with a maximum value of 6.61 ± 0.89 cm. The dry weight, substrate length, cap circumference, and cap length of morel mushrooms in YJ test site were higher than those in XG test site.

Quality of morel mushrooms

The substrate moisture contents in the two test sites ranged from 88% to 90%, and differences among different treatments were not significant ($P > 0.05$) (Figure 8). For ash and crude fiber contents, XG test site presented higher values than those in YJ test site. Regarding crude protein accumulation, variation trend was $T2 > T3 > T1 > T4 > CK$ with a maximum value of 32.73 ± 1.28 g/100 g in XG test site, while variation trend was $T2 > T4 > CK > T1 > T3$ with a maximum value of 32.72 ± 0.92 g/100 g in YJ test site. No significant difference was observed among different treatments for crude protein content in the two test sites ($P > 0.05$). Crude polysaccharide

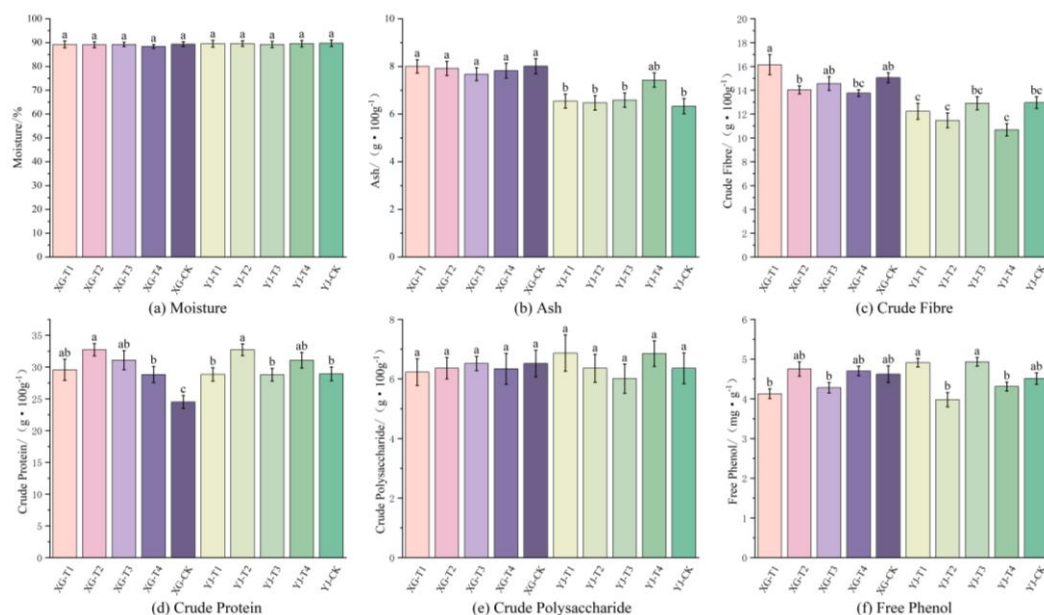


Figure 8. Morel quality indicators.

content ranged from 5 to 7 g/100 g in both test sites with no significant differences among various treatments ($P > 0.05$). For free phenol content, variation trend in XG test site was T2 > T4 > CK > T3 > T1 with contents ranging from 3.98 to 4.93 mg/g. In YJ test site, variation trend was T3 > T1 > CK > T4 > T2 with contents within the range of 3.98 to 4.93 mg/g.

Comprehensive evaluation of the yield and quality of morel mushrooms

PCA was applied to comprehensively assess the yield and quality of morel mushrooms. Moisture, ash, crude fiber, crude polysaccharide, crude protein, free phenol, dry mushroom yield, fresh mushroom yield, cap length, cap circumference, and dry weight of a single mushroom were adopted as variables for PCA. The analysis focused on extracting the first three principal components with eigenvalues of greater than 1. In XG test site, eigenvalues were 5.286, 2.734, and 1.859, while the contribution rates of these principal components to the total variance were 48.1%, 24.9%, and 16.9% for PC1, PC2, and PC3, respectively. Also, the cumulative variance contribution rate of these three components was 89.9%, basically reflecting the information of all

quality variables. The score rankings of different treatments were calculated and followed the trend of XG-T2 > XG-T4 > XG-T1 > XG-CK > XG-T3. In YJ test site, the same indicators were adopted for PCA, and the first three principal components were extracted, all of which had eigenvalues of greater than 1. The eigenvalues for YJ test site were 3.992, 3.291, and 2.692, while the variance contribution rates of these principal components were 36.3%, 29.9%, and 24.5% for PC1, PC2, and PC3, respectively. The cumulative variance contribution rate of these three components was 90.7%, basically reflecting the information of all quality indicators. The score rankings of different treatments were calculated using PCA and the results demonstrated a trend of YJ-T2 > YJ-T3 > YJ-T1 > YJ-CK > YJ-T4 (Figure 9).

Correlation analysis

The results showed that, in protoplast and substrate stages, fresh mushroom yield, dry mushroom yield, and mushroom density were positively correlated with surface soil organic carbon, quick-acting potassium, soil water content, and negatively correlated with surface soil pH and temperature (Figure 10). Increased morel mushroom yields could be attributed, in

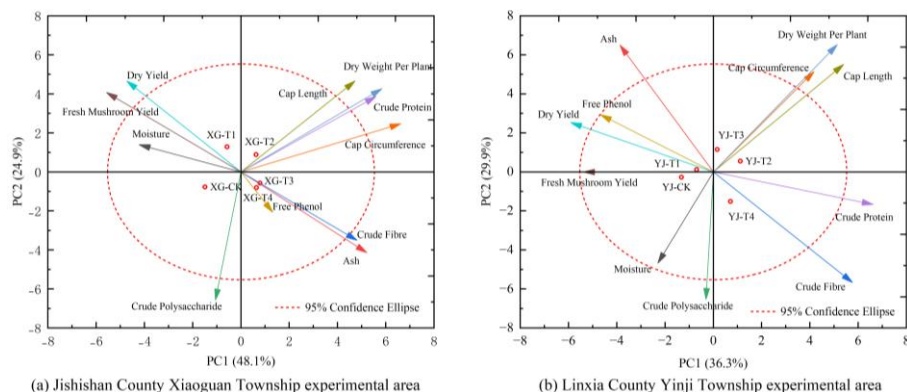


Figure 9. Principal component analysis results.

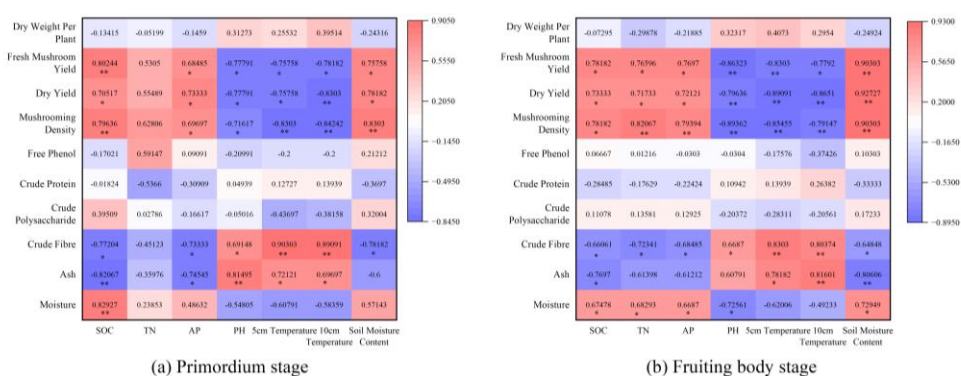


Figure 10. Spearman's correlation analysis between yield quality of morel and soil indicators. * indicated significant difference ($P < 0.05$). ** indicated very significant difference ($P < 0.01$).

part, to soils with abundant organic matters and high water retention capacities [5]. Morel mushroom growth required maintaining soil temperature below 15°C [13]. At lower temperatures, substrate development was slower, resulting in higher quality [6]. However, excessively high soil and ambient temperatures not only halted substrate growth and protocorm emergence, but also, in combination with high humidity, could result in widespread pathogen infection, thereby decreasing yield. The YJ test site employed greenhouse to overcome winter conditions, which resulted in early mushroom emergence, lower temperatures during emergence period, and longer suitable temperature durations for mushroom emergence compared to XG test site. Therefore, the yields were higher in YJ test site. The crude fiber composition of substrate during primary

and substrate stages was negatively correlated with soil nutrients and soil water content and positively correlated with soil temperature (Figure 10), which suggested that increase of the nitrogen content, organic carbon content, and water-holding capacity of soil and decrease of soil temperature to a certain extent decreased the crude fiber composition of substrate. The correlations between ash and crude fiber composition of substrate and soil physicochemical characteristics were similar. Ash content level reflected the selective uptake and accumulation of mineral elements, and this correlation could be attributed to soil differences between the two test areas. Compared to yellow loam, black loam soil had higher amounts of mineral nutrients, making it more conducive to quality formation in morel mushrooms. The moisture content of *F. lamblia* substrate was

found to be positively correlated with soil surface organic carbon content in protocorm stage and positively correlated with organic carbon, quick-acting potassium, total nitrogen, and soil water contents in substrate stage. Also, a negative correlation was observed with soil pH. The results demonstrated that soils with high nutrient contents and water-holding capacities were more conducive to improving the moisture content of morel mushroom fruiting body.

Discussion

During protocorm and substrate stages, a certain soil water content had to be maintained [14]. However, excessively high soil water contents might result in low oxygen state in soil. For aerobic morel mushroom, this could potentially affect yield and quality [15]. In both YJ and XG test sites, soil water contents were basically maintained at about 20% during mycelial stage. At the end of this stage, i.e., after the maturation of the kernels (spores or mycelial aggregates), it was essential to continuously irrigate the soil containing these kernels to promote protocorm formation [16]. In this research, all treatments significantly increased soil water content after mycorrhizal maturation. Although different amounts of irrigation were applied in different treatments, it was observed that, following differential irrigation, soil surface water content initially reached a peak and then decreased to a relatively stable level. Surface soil water content was strongly affected by external environment. During morel mushroom substrate stage, a shaded environment was required throughout the planting period [17]. Due to less solar radiation in the greenhouse, less sensible heat energy was vaporized, and soil evaporation was decreased under the effect of the maintenance of high air relative humidity and small saturated water vapor pressure difference [18]. This resulted in relatively stable soil water contents. Greenhouse air temperature and the soil moisture used for morel mushroom cultivation were found to affect soil temperature [19]. Spearman's correlation analysis presented a

weak correlation between the water content and temperature of soil ($r = 0.454$, $P < 0.01$), which could be attributed to "simultaneous hydrothermal effects" during morel mushroom cultivation. The soil temperature variation trend during each fertility period closely resembled that of ambient temperature. All treatments in this research maintained high relative soil water contents after irrigation, and differential irrigation had minimal impacts on the temperature of soil surface layer at 0 - 10 cm.

The results of comparing soil pH before and after planting revealed that morel mushroom cultivation decreased soil pH, aligning with the previous report [20]. Soil pH was primarily determined by relative concentrations of H^+ and OH^- ions in the soil. Slight fluctuations in soil pH following irrigation were mainly attributable to soluble ion movements within the soil facilitated by water, as well as the stability of relative concentrations of H^+ and OH^- ions in the soil. The carbon source required for morel mushroom growth was primarily provided by exogenous nutrient bags, while nitrogen was supplied by soil [21]. Due to exogenous nutrient bags, soil organic carbon (SOC) accumulated during mycelial stage and a significant amount of organic carbon was consumed by the time mushrooms emerged [22]. In this research, the main planting soils were yellow loam and black soils. Yellow loam had a moderate sandy-clay texture and good permeability, but low nitrogen and organic carbon contents. However, black loam soil primarily consisting of silt particles had higher nitrogen and organic carbon contents. The planting of morel mushrooms increased SOC in both soil types comparing to that before cultivation, which was consistent with the organic carbon change trend reported previously [14]. Soil nitrogen content influenced morel mushroom growth [20]. In this research, soil surface total nitrogen primarily decreased during the mycelium and protocorm stages of morel mushroom development [23]. In line with the findings of Tan *et al.* [22], as morels grew, soil surface total nitrogen gradually rebounded, but total nitrogen content after harvesting were still

lower than that before planting. Different irrigation treatments did not exhibit a clear variation pattern in surface soil organic carbon and total nitrogen contents, which was mainly due to morel mushroom growth in soils with relatively wet surfaces during their development, resulting in low soluble organic carbon and total nitrogen contents. Therefore, the effects of irrigation amount on surface soil organic carbon and total nitrogen contents were not obvious [24]. The content of soil quick-acting potassium reflected the ability of soil to supply potassium [25]. Research has demonstrated that potassium in the upper layer of soil is essential for morel mushroom growth [26]. Potassium content can directly or indirectly enhance morel mushroom yield by decreasing the prevalence of fungal populations in the soil. During morel mushroom growth period, different treatments had minimal impacts on the fast-acting potassium contents of the cultivated surface soil. Irrigation could leach fast-acting potassium from the surface soil. However, in this study, fast-acting potassium content did not exhibit a clear correlation with the amount of irrigation, which was initially attributed to the micro-sprinkler irrigation technology employed in the research, resulting in insignificant differences in leaching among different irrigation amounts. The concentration of readily available potassium in the soil following harvest was greater than that in initial soil composition. Such increase could likely be attributed to the mineral potassium being decomposed by the microbial community of the soil as well as the liberation of organic matter resulting from the breakdown of external nutrient bags [27].

The comprehensive analysis of morel mushroom yield and quality revealed that reducing local irrigation in late mycelial stage decreased fresh and dry mushroom production to certain extents. The treatment with high irrigation resulted in higher number of mushrooms, but the control group (CK) with the highest irrigation was not the optimal treatment in terms of dry weight per plant, cap length, and cap circumference of morel mushrooms. Instead, 90% of local irrigation

amount treatment (T2) was optimal, which might be because excessive irrigation prompted the occurrence of a large number of protoplasts, limiting the amount of nutrients available to individual plants and affecting the agronomic traits of mushrooms. Cap length was one of the criteria for the evaluation of the commercial quality of morel mushrooms and there was a strict limitation on stipe length [28]. T2 treatment resulted in a longer cap compared to other treatments, increasing its commercial value.

Conclusion

This study found that water content at 0–10 cm deep soil layer was increased by increasing irrigation amount, while soil pH exhibited a decreasing trend. However, variations of irrigation amount had minimal effects on soil temperature, organic carbon, total nitrogen, and quick-acting potassium contents. The yield indexes of mushroom density, fresh mushroom yield, and dry mushroom yield of all treatment were increased by increasing micro-sprinkler irrigation, but morel mushroom quality indices exhibited a pattern of initial increase followed by subsequent decrease in response to escalating levels of irrigation. Local irrigation amount exhibited the highest yield, while the quality indexes of 90% of local irrigation amount treatment were optimal. Black loam soil was found to be more conducive to higher morel mushroom yield and quality than yellow loam. Spearman correlation analysis revealed that soil organic carbon, quick-acting potassium, and soil water contents, as well as ambient temperature were positively correlated with high yields of morel mushrooms. Appropriate decrease of soil moisture content and maintaining winter soil temperature of 5–10°C both contributed to the enhancement of morel mushroom quality. Further, principal component analysis showed that 90% of local irrigation amount treatment had the highest score.

Acknowledgements

This work was supported by the Jinan Water Science and Technology Project (Grant No. JNSWKJ202206), National Natural Science Foundation of China (Grant No. 52469011), and Open Fund Grant for the Key Laboratory of Degraded and Unutilized Land Remediation Engineering of Ministry of Natural Resources (Grant No. SXDJ2024-08).

References

- Tietel Z, Masaphy S. 2018. True morels (*Morchella*) nutritional and phytochemical composition, health benefits and flavor: A review. *Crit Rev Food Sci Nutr*. 58(11):1888-1901.
- Pei LY, Liu W, Liu LP, Wang XY, Jiang LX, Chen ZH, *et al.* 2023. Morel (*Morchella* spp.) intake alters gut microbial community and short-chain fatty acid profiles in mice. *Front Nutr*. 10:1237237.
- Sambyal K, Singh RV. 2021. A comprehensive review on *Morchella importuna*: Cultivation aspects, phytochemistry, and other significant applications. *Folia Microbiologica*. 66:147-157.
- Li ZD, Wu L, Wang SW, *et al.* 2021. Production scale and technical points of field cultivation of *Agaricus blazei* in China. *Medicinal Mushrooms*. 29(6):461-465.
- Bian YB. 2024. A brief analysis of scientific and technical problems related to stable and high yield of morels. *Acta Edulis Fungi*. 31(01):31-37.
- He XS. Biological basis, strain isolation and production and high-yield cultivation technology of *Agaricus blazei*. Beijing: Science Press. 2017.
- Meshrama DT, Gorantiwarb SD, Singh NV, Babu KD. 2019. Response of micro-irrigation systems on growth, yield and WUE of Pomegranate (*Punica granatum* L.) in semi-arid regions of India. *Scientia Horticulturae*. 246:686-692.
- Mebrate A, Kippie T, Zeray N, Haile G. 2022. Selected physical and chemical properties of soil under different agroecological zone in Gedeo Zone, Southern Ethiopia. *Heliyon*. 8(12):e12011.
- Artuso DR, Moterle DF, Santos DR, Tiecher T. 2024. Potassium distribution in soil profiles under no-tillage system. *Revista Brasileira de Ciencia do Solo*. 48:e0230125.
- Su DW, Song FF, Luo HL, Lin H, Lin DM, Liu PH, *et al.* 2022. Effect of different rotation systems on production and quality of black morel (*Morchella importuna*). *Agronomy (Basel)*. 12(8):1744.
- Li Y, Lin W, Chen J, Lin J, Feng R, Yan J, *et al.* 2024. Nitrates and microbiome components engaged in denitrification within soil regulate *Morchella* spp. Growth. *Horticulturae*. 10(9):905.
- Kobori R, Yakami S, Kawasaki T, Saito A. 2021. Changes in the polyphenol content of red raspberry fruits during ripening. *Horticulturae*. 7(12):569.
- Benucci GMN, Longley R, Zhang P, Zhao Q, Bonito, G, Yu F. 2019. Microbial communities associated with the black morel *Morchella sextelata* cultivated in greenhouses. *Peer J*. 7:e7744.
- Liu Q, Ma H, Zhang Y, Dong C. 2018. Artificial cultivation of true morels: current state, issues and perspectives. *Crit Rev Biotechnol*. 38(2):259-271.
- Ower RD, Mills GL, Malachowski JA. 1985. Cultivation of morels. NEOGEN CORP. 1985.
- Shahid H, Hassan S. 2021. Ecological characterization of Morel (*Morchella* spp.) habitats: A multivariate comparison from three forest types of district Swat, Pakistan. *Acta Ecologica Sinica*. 41(1):1-9.
- Tong B, Guo J, Xu H, Wang Y, Li H, Bian L, *et al.* 2022. Effects of soil moisture, net radiation, and atmospheric vapor pressure deficit on surface evaporation fraction at a semi-arid grass site. *Sci Total Environ*. 849:157890.
- Boddy L, Buntgen U, Egli S, Gange AC, Heegaard E, Kirk PM, *et al.* 2014. Climate variation effects on fungal fruiting. *Fungal Ecol*. 10:20-33.
- Liu Wy, Guo Hb, Bi KX, Sibirina LA, Qi XJ, Yu XD. 2022. Determining why continuous cropping reduces the production of the morel *Morchella sextelata*. *Front Microbiol*. 13:903983.
- Lohberger A, Spangenberg JE, Ventura Y, Bindschedler S, Verrecchia EP, Bshary R, *et al.* 2019. Effect of organic carbon and nitrogen on the interactions of *Morchella* spp. and bacteria dispersing on their mycelium. *Front Microbiol*. 10:124.
- Tan H, Kohler A, Miao R, Liu T, Zhang Q, Zhang B, *et al.* 2019. Multi-omic analyses of exogenous nutrient bag decomposition by the black morel *Morchella importuna* reveal sustained carbon acquisition and transferring. *Environ Microbiol*. 21(10):3909-3926.
- Tan H, Yu Y, Tang J, Liu T, Miao R, Huang Z, *et al.* 2021. Build your own mushroom soil: Microbiota succession and nutritional accumulation in semi-synthetic substratum drive the fructification of a soil-saprotrophic morel. *Front Microbiol*. 12:656656.
- Cenkseven S, Kizildag N, Koçak B, Sagliker HA, Darici C. 2017. Soil organic matter mineralization under different temperatures and moisture conditions in Kiziladag Plateau, Turkey. *Sains Malaysiana*. 46:763-771.
- Molavi R, Baghernejad M, Ghasemi-Fasaei R, Zarei M. 2020. Release characteristics of potassium from native reserves of some calcareous soils of Iran and their relationship with yield and potassium uptake by ryegrass (*Lolium perenne* L.). *Soil Res*. 58(8):770-778.
- Zhang Y, Sun S, Luo D, Mao P, Rosazlina R, Martin F, *et al.* 2023. Decline in morel production upon continuous cropping is related to changes in soil mycobiome. *J fungi (Basel)*. 9(4):492.
- Grunert O, Hernandez-Sanabria E, Buysens S, De Neve S, Van Labeke MC, Reheul D, *et al.* 2020. In-depth observation on the microbial and fungal community structure of four contrasting tomato cultivation systems in soil based and soilless culture systems. *Front Plant Sci*. 11:520834.
- Qiu Z, Ren S, Zhao J, Cui L, Li H, Jiang B, *et al.* 2023. Comparative analysis of the nutritional and biological properties between the pileus and stipe of *Morchella sextelata*. *Front Nutr*. 10:1326461.
- Wang GS, Ran LJ, Tian S, Duan FY. 2019. Summary of high-quality and high-efficiency cultivation technology of morel mushrooms in outdoor greenhouses. *China Edible Mushroom*. 38(3):103-106.